Foregut and reproductive tract anatomy of three species of the *Strombina*-group (Buccinoidea: Columbellidae)

Anatomía del tubo digestivo y del tracto reproductor en tres especies del grupo Strombina (Buccinoidea: Columbellidae)

Helena FORTUNATO*

ABSTRACT

This paper reports for the first time anatomical data for three species of the *Strombina*-group sensu Jung, 1989: *Bifurcium bicanaliferum*, *Sincola (Dorsina) gibberula* and *Clavistrombina clavulus*. Anatomical data for the foregut and reproductive tracts were determined from gross dissections mainly of living specimens. Both the anterior digestive tract and the reproductive systems of the three species are similar in their general plan and conform with what is known for columbellids and neogastropods in general.

Differences among the three species are mostly within accessory structures. None of them presents either a bursa copulatrix or a prostate gland. The ingestive gland is also absent. *C. clavulus* males present an open reproductive system with a diverticulum communicating the vas deferens with the body cavity. This species also presents a separated albumen gland, whereas in both *S. gibberula* and *B. bicanaliferum* only an internal septum separates this gland from the capsule gland. *Bifurcium* and *Sincola* both appear during the early Miocene of Dominican Republic, which could bear on their anatomical similitude, whereas *Clavistrombina* is a Recent genus of the eastern Pacific. More studies of other species of these genera are needed in order to better understand possible evolutionary connections of these body plans.

RESUMEN

Se describe por vez primera datos anatómicos de tres especies del grupo *Strombina* sensu Jung, 1989: *Bifurcium bicanaliferum*, *Sincola (Dorsina) gibberula* y *Clavistrombina clavulus*. Los datos anatómicos se determinaron a partir de disección de especimenes vivos. Los tractos digestivo y reproductor de las tres especies estudiadas son similares en su estructura general y se corresponden con los conocidos para columbellidos y neogasterópodos en general.

Las diferencias se concentran en las estructuras accesorias. Ninguna especie presenta bolsa copulatriz, próstata o glándula ingestiva. Los machos de *C. clavulus* tienen un sistema reproductor abierto con un divertículo que comunica el vaso deferente con la cavidad del cuerpo. Esta especie tiene una glándula del albumen separada, mientras que en *S. gibberula* y en *B. bicanaliferum* sólo un septo la separa de la de la cápsula. Tanto *Bifurcium* como *Sincola* aparecieron durante el Mioceno temprano en la República Dominicana, lo cual puede explicar su similitud anatómica, mientras que *Clavistrombina* es una especie reciente del Pacífico este. Se precisan más estudios sobre otras especies de estos géneros para una mejor comprensión de las posibles conexiones evolutivas entre estas características anatómicas.

* Center for Tropical Anthropology and Paleoecology, Smithsonian Tropical Research Institute, P.O. Box 169, Balboa, Panama R P, e-mail: fortunae@ancon.si.edu

INTRODUCTION

Neogastropods are generally considered the most highly evolved prosobranch gastropods. This large order, with more than 1000 recent and fossil genera and subgenera (TAYLOR AND SOHL, 1962), is characterized by a shell with an elongate siphonal canal and rachiglossate or toxoglossate radula. The classification and biology of neogastropods has been the focus of many authors as it contains several extremely important groups, both economically and biologically (ADAMS AND ADAMS, 1858; THIELE, 1929; RISBEC, 1954; FRETTER AND GRAHAM, 1962; PONDER, 1973; HARASEWYCH, 1984; BRIGHT AND ELLIS, 1990; KOOL, 1993).

Neogastropods have a rather similar anatomical organization. This was shown to be true for the reproductive systems of the Muricidae, Buccinidae, and Nassaridae (FRETTER, 1941; FRETTER AND GRAHAM, 1962). Families such as Olividae, Columbellidae, Fasciolaridae and Turridae are less studied (MARCUS AND MARCUS, 1959, 1960, 1962; SMITH, 1967; HOUSTON, 1976; KANTOR, 1991; SYSOEV, 1991). The foregut of some of these groups shows signs of simplification, as in the Muricidae (GRAHAM, 1949), whereas others have features of the Archaeogastropoda (BROWN, 1969; PONDER, 1972), or have become secondarily complex (PONDER, 1970).

The family Columbellidae, one of the groups traditionally included in the buccinoid neogastropods, appears during the Eocene (RADWIN, 1977a). Although relatively younger than most other neogastropod taxa, which appear in the Cretaceous, is one of the most diverse and abundant, with almost four hundred recent species (TAYLOR, MORRIS AND TAYLOR, 1980). Contrasting with this, there aren't that many works dealing with the anatomy of this group, as stated above. THIELE (1929) and RADWIN (1977a, 1977b) use radular features to subdivide the family into two subfamilies. RISBEC (1954) and especially MARCUS AND MARCUS (1962, 1964) give the first anatomical descriptions of several columbellid species. Later, HOUSTON (1976) and HOUSTON AND HATFIELD (1981) described a couple more species. Several other species were studied in relation to evolution of herbivory in gastropods (HATFIELD,1979; HARASEWYCH, 1990; KANTOR AND MEDINSKAYA, 1991; MEDINSKAYA, 1992; MEDISNKAYA, 1993; GURALNICK AND DE MAINTENON, 1997; DE MAINTENON, 1999).

The Panamic province has a rich assemblage of columbellids many of which have a very interesting evolutionary history related to the rise of the Central American Isthmus . This is the case with the *Strombina*-group sensu Jung, 1989. The group consists of five genera and includes most taxa classified as *Strombina* by earlier workers. JUNG (1989) splits this genus and proposes several new genera. Despite the splitting, the group is still known in the malacological jargon as the *Strombina*-group, following JUNG's (1989) designation. The group needs extensive systematic revision (DE MAINTENON, 1994) and the relations of these genera to other tropical American columbellids and to each other is still poorly unknown (RADWIN, 1977a, 1977b; JUNG, 1989). Nevertheless, preliminary cladistic analyses based on shell morphology and anatomy strongly support the hypothesis of a separate columbellid clade composed by these five genera, as well as the validity of JUNG's (1989) major genera and subgenera (FORTUNATO AND JUNG, 1995).

The *Strombina*-group is amongst the most abundant and diverse Neogene gastropods, and is represented by more than 30 living species in the eastern Pacific but only four in the Caribbean, where they suffered a massive extinction at the end of the Pliocene (JUNG, 1989; JACKSON, JUNG, COATES AND COLLINS, 1993; JACKSON, JUNG AND FORTUNATO, 1996; FORTUNATO, 1999).

The *Strombina*-group has been used as a model taxon to study changing species morphology and diversity during the gradual emergence of the Isth-
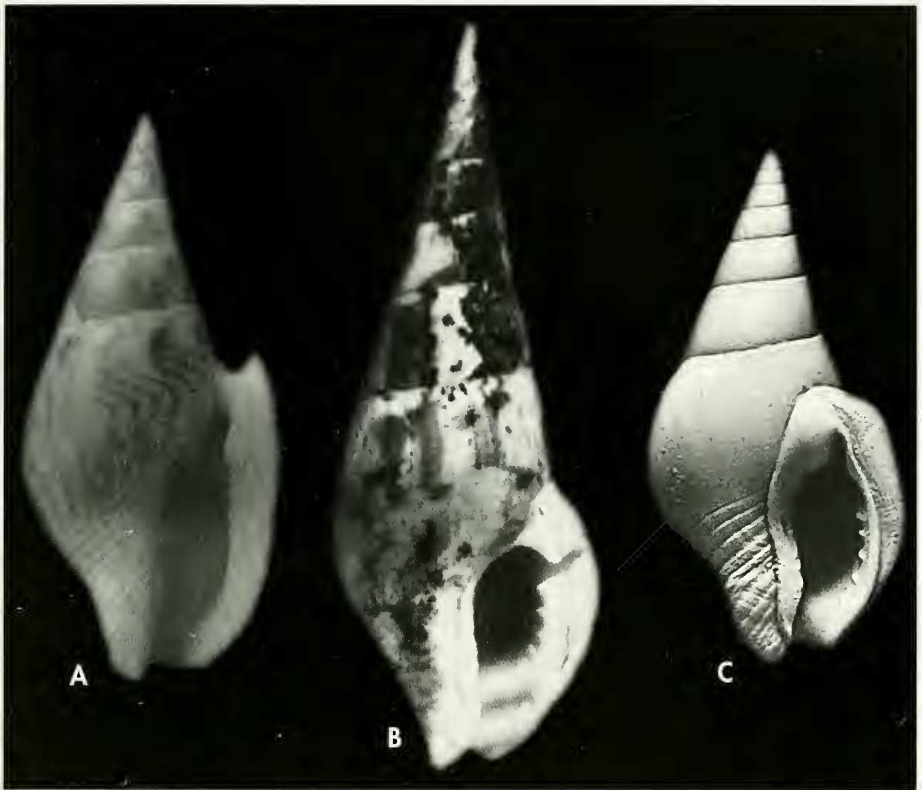
Figure 1. Portraits of the species studied. A: *Bifurcium bicanaliferum* (B. G. Sowerby I, 1832); B: *Sincola (Dorsina) gibberula* (B. G. Sowerby I, 1832); C: *Clavistrombina clavulus* (B. G. Sowerby I, 1834).
Figura 1. Especies estudiadas. A: Bifurcium bicanaliferum *(B. G. Sowerby I, 1832); B:* Sincola (Dorsina) gibberula *(B. G. Sowerby I, 1832); C:* Clavistrombina clavulus *(B. G. Sowerby I, 1834).*

mus of Panama (JACKSON, JUNG AND FORTUNATO, 1996; FORTUNATO, 1998, 1999). In spite of this, very little is known of the biology of these gastropods (CIPRIANI AND PENCHASZADEH, 1993; CIPRIANI, FORTUNATO AND RODRIGUEZ, 1996; FORTUNATO, PENCHASZADEH AND MILOSLAVICH, 1998; FORTUNATO, 2002). There are no anatomical studies of any of its species, except for some references to the type of radulae (RADWIN, 1978; HOUBRICK, 1983; EMERSON, 1993). The objective of this paper it is to present the gross anatomy of the digestive and reproductive systems of three species: *Bifurcium bicanaliferum* (G. B. Sowerby I, 1832), *Sincola (Dorsina) gibberula* (G. B. Sowerby I,

1832) and *Clavistrombina clavulus* (G. B. Sowerby I, 1834). *B. bicanaliferum* is the only living species of this genus otherwise known from Miocene deposits of the Caribbean. *S. gibberula* is one of the three extant species of this genus, also known from Miocene deposits of the Caribbean. *C. clavulus* is the only species of this monotypic genus and has no known fossil record (JUNG, 1989). All three species inhabit the shallow water (up to 40 m deep) coasts of the eastern Pacific. Whereas the first two species can be found in muddy and sandy beaches, the third prefers rocky environments. In spite of the fact that all three species have a very wide distribution, ranging from the Gulf of California

Table I. Summary of dimensions of several organs for the three species discussed here. Measurements were made with fixed specimens using light microscopy.
Tabla I. Resumen de las dimensiones de varios órganos de las tres especies estudiadas. Las medidas fueron hechas a partir de especímenes fijados con un microscopio óptico.

Genus and species	Length of penis (mm)	Length of proboscis (mm)	Length (mm)	Radulae				Opercula	
				N. of lateral teeth	Size of lateral teeth (µm)	N. of medial plate	Size of medial plate (µm)	Length (mm)	Width (mm)
Bifurcium bicanaliferum	11	10	12	360	79	180	30	1.2	1
Sincola gibberula	7	5	15	450	53	225	20	1.5	1
Clavistrombina clavulus	12	7	10	418	68	209	26	4	2

through Peru, *C. clavulus* is much less abundant than the other two species. All three species are scavengers and have planktotrophic larvae (FORTUNATO ET AL., 1998; FORTUNATO, 2002).

MATERIAL AND METHODS

All work was done with live collected specimens. Collections were done by hand during low tides and by trawling from small boats. Both live and preserved in 5% buffered formalin material was used for this study. About 10 specimens of both sexes from each studied species were dissected. Soft parts were removed from the shells with a vise after the animals have been relaxed with menthol crystals added to the seawater. Before dissecting, material was submerged in Methylene blue to delineate tissues and organs for gross anatomy study. Histological sections were done to study the proboscises. Standard histological techniques were used, the tissues infiltrated with paraffin and sectioned at 7 µm. Transverse sections of of the proboscis were stained with Hematoxylin/eosin (HUMASON, 1962). Measurements of penises, proboscises, and radular teeth were done in fixed specimens using light microscopy and a millimeter ocular . Radulae were removed and cleaned with warm 10% KOH until completely free of tissue. Opercula were treated with 37% hydrogen peroxyde. Both radulae and opercula were coated with gold-palladium, and examined under a JEOL HMS-5300LV Scanning Electron Microscope.

RESULTS

1. Morphology of the anterior alimentary tract

Bifurcium bicanaliferum (Fig. 1A)

The operculum (Fig. 2A) is yellowish, rounded, and small (1 mm long and 1.2 mm wide) (Table I). It is very thin and transparent with a proteinaceous consistency. The growth rings are evenly spaced and it has an antero-posterior located nucleus.

The animal has a long, very mobile proboscis (prb) tapering towards a small slit-like mouth opening (mo) (Fig. 4). When resting, the basal part of the proboscis retracts into a tubular fold of the body wall, the proboscis sheath. The proboscis measures about 10 mm (in a fixed animal) (Table I) and is of pleurembolic type, typical of a scavenger and predatory life style.

The mouth leeds to the buccal cavity which occupies the first portion of the
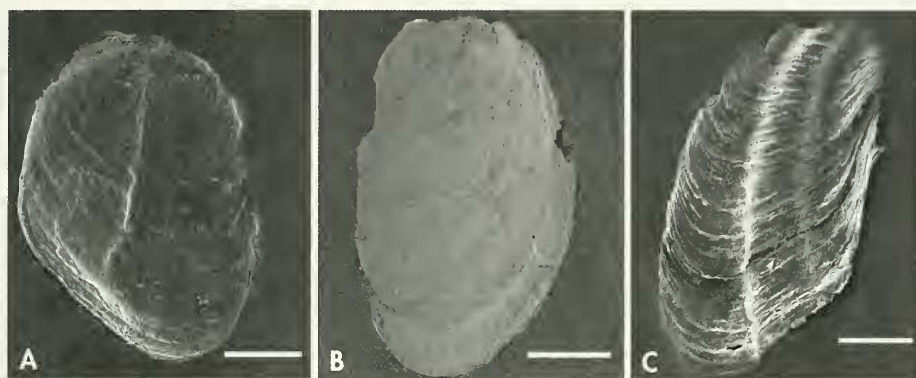
Figure 2. Scanning electron micrographs of opercula. A: *Bifurcium bicanaliferum*; B: *Sincola (Dorsina) gibberula*; C: *Clavistrombina clavulus*. Scale bar 50 µm.
Figura 2. Microfotografías al MEB de opérculos. A: Bifurcium bicanaliferum; *B:* Sincola (Dorsina) gibberula; *C:* Clavistrombina clavulus. *Escalas 50 µm.*

proboscis. Here the odontophore and the radular sac are located. The rachiglossate type radula (1+1+1) (Fig. 3A) is about 12 mm in length (Table I). The radular ribbon is typically collumbellid in shape, narrow, and has two lateral rows of 180 teeth. The median plate, or rachidian tooth, is almost rectangular, long and has rounded edges. Each median plate is 30 µm in length. The lateral teeth have a sigmoid shape and are separated from the rachidian by a large inter-space. Each lateral tooth measures 79 µm in length. They have a wide base, a shaft and two hooked cusps at the tip. A single blunt hook appears in the middle of the tooth shaft. The radula and several layers of the surbradular membrane together form the radular sheath at the end of which the radula is secreted.

The anterior oesophagus, (Fig. 4; aoe), starts at the posterior end of the buccal cavity after separating from the radular sac. Inside the proboscis, the anterior oesophagus has a ventral position. Once it leaves the proboscis, it continues towards the neural ring. This section of the oesophagus is adhered up to its middle through a connective tissue layer to the proboscis sheath. Just after the neural ring, the anterior oesophagus expands in diameter forming the Valve

of Leiblein (vle) or oesophageal bulb. The valve has a reddish natural coloration and a pear shape. The oesophageal bulb is surrounded by the large salivary glands (sgl). These are paired, yellowish glands and they are not attached to the valve. These glands are lobed and the lobes are held together by strong strands of tissue. The salivary ducts (sd) leave the glands and enter the lateral walls of the anterior oesophagus just before the expansion that represents the oesophageal bulb. The ducts follow the anterior oesophagus and discharge their secretions in the buccal mass. The oesophageal bulb signals the beginning of the mid-oesophagus (moe). This bulbous expansion prevents the food from being sucked forward.

The beginning of the mid-oesophagus is narrow. After traversing the neural ring, it makes an S-shape curve after which it begins to engross. The large Gland of Leiblein (gle), or foregut gland, enters directly into the mid-oesophagus without a delimited duct. This unpaired gland has a V-shape and is dark brown. After the insertion of the foregut gland, the oesophagus continues to enlarge becoming the posterior oesophagus (poe) that ends in the stomach.

The proboscis is very long and its wall is composed of a thin outer layer of cuticle (cut) (Fig. 5). The cells here are cubic with a big central nucleus. The next layer is composed of longitudinal muscles (lml) followed by a layer of helical muscle tissue (hml). The subradular cartilages (sc), located within the radular sac (rs), have big cells with a central nucleus. The anterior oesophagus (aoe) is lined with a layer of columnar epithelium interspersed with mucous ciliated cells. The salivary ducts (sd) are located laterally relative to the anterior oesophagus.

Sincola (*Dorsina*) *gibberula* (Fig. 1B)

The operculum of this species (Fig. 2B) is very similar to the anterior one. It is oval shaped, small for the overall size of the animal (1mm long, 1.5 mm wide) (Table I), and yellowish. Its consistency is proteinaceous and it is somewhat thin and transparent. The growth rings are evenly spaced and it has an antero-lateral located nucleus.

Figure 6 shows a short (5 mm) pleurembolic type proboscis (prb) (Table I) that ends in a small slit-like mouth opening (mo). The proboscis in this species is almost translucent. Its basal part retracts into a tubular fold of the body wall, the proboscis sheath.

The mouth leeds to the buccal mass where the odontophore and the radular sac are located. The rachiglossate type radula (1+1+1) (Fig. 3B) is about 15 mm in length (Table I). The typically colum-bellid radular ribbon is narrow, and has two lateral rows of 225 teeth. The rachidian tooth is almost square in shape, narrow, with rounded edges. It measures 20 µm. The sigmoid lateral teeth are separated from the median plate by a large inter-space. Lateral teeth have a wide base and a shaft with two hooked cusps at the tip. Lateral teeth measure 53 µm. The hook in the middle of the tooth shaft is better delineated here than in the previous species. The radula is constantly being secreted at the end of the radular sheath, formed by the radula itself and the layers of the subradular membrane.

The anterior oesophagus (Fig. 6; aoe) begins at the posterior end of the buccal mass and runs dorsally inside the pro-boscis. The Valve of Leiblein (vle) or oesophageal bulb consists of a small expansion of the oesophagus just before the neural ring has a reddish natural coloration and a pear shape and is surrounded by the large salivary glands (sgl). These paired, creamy glands are not connected in any way to the valve. These glands are lobed and the lobes are held together by strong strands of tissue. The long and curved salivary ducts (sd) leave the glands and enter directly into the anterior oesophagus through the posterior lateral walls of the proboscis. The ducts run laterally inside the oesophagus and discharge their secretions into the buccal mass. The mid-oesophagus (moe) begins after the oesophageal bulb. The mid-oesophagus is thick in most of its length. The Gland of Leiblein (gle), or foregut gland, enters into the mid-oesophagus through a small, narrow duct. This is a small, light brown, unpaired organ, with a conic shape. The posterior oesophagus (poe), that starts after the insertion of the foregut gland, ends in the stomach.

The proboscis walls have an outer layer of cuticle (cut) (Fig. 7). The cells of the cuticle are big, cubic, and have a prominent central nucleus. The next layer is composed of helical muscles (hml) followed by a layer of longitudi-nal muscle tissue (lml).

The presence of abundant connec-tive tissue (ct) is noticeable at this level. The subradular cartilages (sc), located within the radular sac (rs), have big cells with a prominent nucleus. Remnants of radular teeth can also be observed inside the radular sac. The salivary ducts (sd) are located on both sides of the anterior oesophagus (aoe). The later has an internal layer of columnar epithelium interspersed with mucous ciliated cells.

Figure 3. Scanning electron micrograph of radulae. A: *Bifurcium bicanaliferum*; B: *Sincola (Dorsina) gibberula*; C: *Clavistrombina clavulus*. Scale bar 100 μm.
Figura 3. Microfotografías al MENB de rádulas. A: Bifurcium bicanaliferum; *B:* Sincola (Dorsina) gibberula; *C:* Clavistrombina clavulus. *Escalas 100 μm.*

Clavistrombina clavulus (Fig. 1C)

The operculum (Fig. 2C) of this species is quite different from the two described before. It has a lenticular shape, brownish color, and is four millimeters long and two millimeters wide (Table I). It is relatively thick with a corneous consistency. The growth rings are evenly spaced and it has an antero-posterior located nucleus, and exhibits a ridge in the middle which gives it a very uncommon aspect.

Figure 8 shows a short proboscis (prb) that ends in a small slit-like mouth opening (mo). At rest, the basal part of the proboscis retracts into the proboscis sheath formed by a tubular fold of the body wall. The proboscis measures seven millimeters (in a fixed animal) (Table I) and is of pleurembolic type.

The mouth ends in the buccal mass located in the first section of the proboscis, and where the odontophore and the radular sac are located. The radula is 10 mm in length (Table I) and is rachiglossate (1+1+1) (Fig. 3C). The radular ribbon has a collumbellid shape, is narrow, and is composed of two lateral rows of 209 teeth. The median plate, or rachidian tooth, is almost square, with rounded edges. The median plate is 26 μm in length. The lateral teeth are sigmoid, and separated from the median plate by a very large inter-space. These teeth are 68 μm in length. The lateral tooth is composed of a narrow base, a shaft with a single hook in the middle, and two hooked cusps at the tip. The radular teeth are secreted at the end of the radular sheath. The later is formed by the radula itself and several layers of the surbradular membrana bundled together.

The short anterior oesophagus (Fig. 8; aoe) starts at the posterior end of the buccal cavity after separating from the radular sac. It runs laterally and expands into the oesophageal bulb or Valve of Leiblein (vle) shortly after leaving the proboscis. The valve is small, somewhat elongated, and translucent. The paired salivary glands (sgl) have a yellowish color and surround the oesophageal bulb. The lobes of the salivary glands are quite big. They are held together by connective tissue. The salivary ducts (sd) are long and curved. They leave the glands and enter the lateral walls of the proboscis, almost at one third of its length. They continue on the inside of the proboscis until they reach the buccal cavity where they discharge their secretions. The oesophageal bulb delimits the beginning of the mid-oesophagus (moe).

The mid-oesophagus is quite narrow up to the section where the short duct of the Gland of Leiblein (gle) enters it. This gland is dark brown and elongated,

accompanying the posterior oesophagus (poe) almost in its entirely length. The posterior oesophagus thickens slightly before entering in the stomach.

The foot (ft) is very thick and short (Fig. 9). The short proboscis is quite muscular. The walls have a thick outer layer of cuticle (cut). Inside the proboscis (prb) large mucous glands (glm) can be seen. The anterior oesophagus (aoe) has on both sides the large openings of the salivary ducts (sd).

2. Morphology of the reproductive systems

Bifurcium bicanaliferum (Figs. 10, 13)

The bright yellow ovary (Fig. 10; ov) is located laterally relative to the digestive gland from which is separated by a layer of connective tissue. The oviduct (ôvd) is relatively short; it runs parallel to the body wall and enters the albumen gland (alb) located near the kidney. The capsule gland (cgl) follows. At first glance, the two glands are almost indistinguishable from each other. Nevertheless, transversal and longitudinal sections of both organs show the presence of a small internal septum dividing both glands. Histological sections show the presence of more glandular tissue in the section corresponding to the albumen gland than after the internal septum. The vestibule (vsb) is very short and is located at the end of the capsule gland, followed by the female aperture (fop) which drains directly to the mantle cavity next to the anus.

The testis (Fig. 13; tes), share with the digestive gland the posterior part of the visceral cavity. The testis are located laterally to the digestive gland and from it the short testicular duct (ted) runs parallel to the stomach; after a short while it becomes extremely convoluted and becomes the seminal vesicle (sev). In the posterior region of the body mass, the seminal vesicle straightens out again and becomes the vas deferens (vd), a very thin and quite long duct that runs parallel to the rectum and the body wall until it reaches the base of the penis (pen). It enters the penis becoming the penial duct (pd), which runs centrally inside it. It is a convoluted tube that opens at the tip of the male organ. In resting animals, the penis is curved backwards along the right side of the body and rests in the penial pouch. The penis measures 11 mm long and is thickened in its middle part, tapering towards the tip. Its ventral side is somewhat wrinkled and dorso-ventrally flattened.

Sincola (*Dorsina*) *gibberula* (Figs. 11, 14)

The yellowish colored ovary (Fig. 11; ov) is lateral to the digestive gland, and separated from these by connective tissue. Follows a short and somewhat sinuous oviduct (ovd) that runs parallel to the body wall and enters the albumen gland (alb). A small external membrane connects the albumen and the capsule glands (cgl). Histological sections show the presence of a relatively deep internal septum dividing the two regions. The tissues present in both are also different, the first being much more glandular than the second. Both organs are located near the kidney. The vestibule (vsb) is well delineated in this species and runs from the anterior region of the capsule gland parallel to the rectum until it ends in the female opening (fop) located contiguous to the anus.

The testis (Fig. 14; tes) are located in the visceral cavity near the digestive gland, in a lateral position. The testicular duct (ted) is relatively long, runs parallel to the stomach and, soon after leaving the testis, starts to convolute,
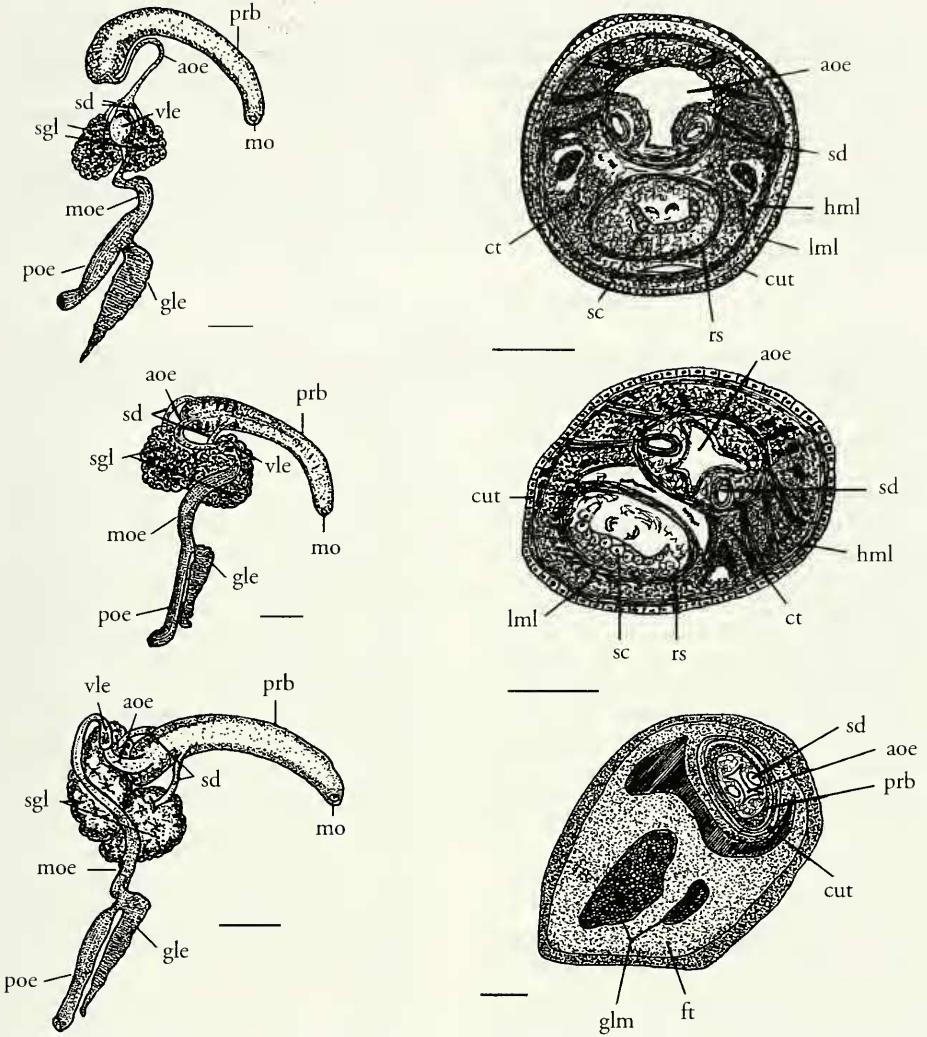
Figures 4, 5. *Bifurcium bicanaliferum*. 4: macromorphology of the anterior alimentary tract; 5: transverse section of proboscis. Figures 6, 7. *Sincola (Dorsina) gibberula*. 6: macromorphology of the anterior alimentary tract; 7: transverse section of proboscis. Figures 8, 9. *Clavistrombina clavulus*. 8: macromorphology of the anterior alimentary tract; 9: transverse section of proboscis. Abbreviations. aoe: anterior oesophagus; ct: connective tissue; cut: cuticle; ft: foot; gle: gland of Leiblein; glm: gland of mucus;hml: helical muscle; lml: longitudinal muscle; mo: mouth; moe: middle oesophagus; poe: posterior oesophagus; prb: proboscis; rs: radular sac; sc: subradular cartilages; sd: salivary duct; sgl: salivary gland; vle: valve of Leiblein. Scale bars, 4, 6, 8: 2 mm; 5, 7, 9: 250 μm

Figuras 4, 5. Bifurcium bicanaliferum. *4: macromorfología del tracto alimentario anterior; 5: sección transversal de la probóscide. Figuras 6, 7.* Sincola (Dorsina) gibberula. *6: macromorfología del tracto alimentario anterior; 7: sección transversal de la probóscide. Figuras 8, 9.* Clavistrombina clavulus. *8: macromorfología del tracto alimentario anterior; 9: sección transversal de la probóscide. Abreviaturas. aoe: esófago anterior; ct: tejido conectivo; cut: cutícula; ft: pie; gle: glándula de Leiblein; glm: glándula del mucus;hml: múscula helicoidal; lml: múscula longitudinal; mo: boca; moe: esófago medio; poe: esófago posterior; prb: probóscide; rs: saco radular; sc: cartílagos subradulares; sd: conducto salivar; sgl: glándula salivar; vle: válvula de Leiblein. Escalas, 4, 6, 8: 2 mm; 5, 7, 9: 250 μm*

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forming the seminal vesicle (sev). This has a whitish coloration and is located laterally to the stomach. At the posterior end, the gonadal duct becomes straight again forming the vas deferens (vd). The later is thick, not very long and runs parallel to the rectum along the body walls and enters the base of the penis (pen). Here it forms the penial duct (pd) that runs along and inside the penis, opening at its tip. The penis of this species is quite short, only seven millimeters long, and thickened throughout most of its way. Its surface is smooth and flattened in the dorso-ventral region. At rest, it is tucked in the penial pouch located in the dorsal region of the body wall.

Clavistrombina clavulus (Figs. 12, 15)

The female ducts of this species (Fig. 12) show several differences from the two previous species. The ovary (ov) is yellow and has a lateral position relative to the digestive gland, from which it is separated by a layer of connective tissue. The long oviduct (ovd) is sinuous and divided into two parts. It runs parallel to the body wall, curves and enters the completely delimited albumen gland (alb), which is located laterally to the kidney. After traversing the albumen gland, the gonadal duct leaves it, curves again and enters the capsule gland (cgl). The later has a bean shape and is located anteriorly to the kidney. From its posterior section starts the long and plain vestibule (vsb), which runs parallel to the rectum and opens near the anus in the female opening (fop).

Both the testis (Fig. 15; tes) and the digestive gland are located posteriorly in the visceral mass. A short testicular duct (ted) curves once after leaving the testis, and soon becomes coiled forming the seminal vesicle (sev). Both the testicular duct and the seminal vesicle are located parallel to the stomach. After the seminal vesicle, the duct becomes straight again forming a long conduct, the vas deferens (vd) which runs parallel to the rectum and ventrally gives origin to a short diverticulum (dv). The later connects with the mantle cavity through an opening (omc). Immediately after the diverticulum, the vas deferens enters the base of the penis (pen) and becomes the penial duct (pd), running centrally and appears as a convoluted and long tube which opens at the tip of the penis. The penis is very long, over 12 mm in length, smooth, and flattened dorso-ventrally. As in the two previous species, the penis rests in the penial pouch located in the posterior dorsal region of the body.

DISCUSSION

Both the anterior alimentary tract and the reproductive systems of the three studied species are similar in their general plan. In what concerns the anterior alimentary tract, the most important difference lies in the insertion of the salivary ducts, which in *B. bicanaliferum* occurs in the anterior oesophagus just before the Valve of Leiblein, whereas in both *S. gibberula* and *C. clavulus* it happens in the posterior region of the proboscis. *B. Bifurcium* also presents a much longer proboscis and anterior oesophagus, as well as a larger oesophageal bulb than the other two species, in spite of the fact that the animal in itself is smaller in size (range size for *B. bicanaliferum*: 9–13 mm; *S. gibberula*: 9–12 mm; *C. clavulus*: 14–25 mm).

At the level of the reproductive systems, *C. clavulus* shows several differences mostly within the accessory structures. Of particular interest is the existence of a well defined albumin gland in females and a mantle opening (the diverticulum) in the males. The later is of special interest as it bears on the evolution of the open reproductive system. This
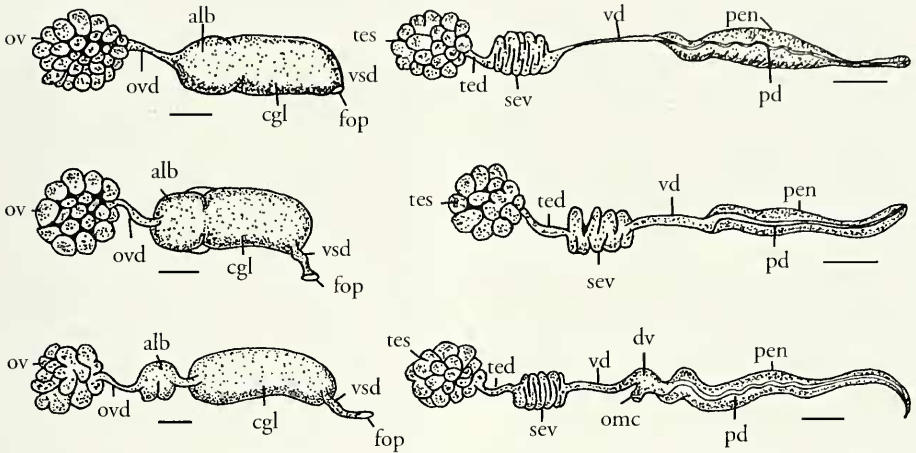
Figures 10-12. Macromorphology of the female ducts. 10: *Bifurcium bicanaliferum*; 11: *Sincola (Dorsina) gibberula*; 12: *Clavistrombina clavulus*. Figures 13- 15. Macromorphology of the male ducts. 13: *Bifurcium bicanaliferum*; 14: *Sincola (Dorsina) gibberula*; 15: *Clavistrombina clavulus*. Abbreviations: alb: albumen gland; cgl: capsule gland; dv: diverticulum; fop: female opening; omc: opening in mantle cavity; ov: ovary; ovd: oviduct; pd: penial duct; pen: penis; ted: testicular duct; tes: testis; sev: seminal vesicle; vd: vas deferens; vsb: vestibule. Scale bars. 10, 11: 3 mm; 12: 5 mm; 13, 14: 4 mm; 15: 10 mm.

Figuras 10-12. Macromorfología de los conductos femeninos. 10: Bifurcium bicanaliferum; *11:* Sincola (Dorsina) gibberula; *12:* Clavistrombina clavulus. *Figuras 13- 15. Macromorfología de los conductos masculinos. 13:* Bifurcium bicanaliferum; *14:* Sincola (Dorsina) gibberula; *15:* Clavistrombina clavulus. *Abreviaturas: alb: glándula del albumen; cgl: glándula de la cápsula; dv: divertículo; fop: abertura femenina; ov: ovario; omc: abertura en la cavidad del manto; ovd: oviducto; pd: conducto peneal; pen: pene; ted: conducto testicular; tes: testis; sev: vesícula seminal; vd: vaso deferente; vsb: vestíbulo. Escalas. 10, 11: 3 mm; 12: 5 mm; 13, 14: 4 mm; 15: 10 mm.*

condition is typical in most mesogastropods and is considered to be the primitive state (JOHANSSON, 1942; FRETTER, 1946). In spite of the fact that most neogastropods present a fused reproductive duct, the presence of an opening to the mantle cavity occur in several columbellids, olivids, muricids, buccinids, and turrids (MARCUS AND MARCUS, 1959, 1962; SMITH, 1967; HOUSTON, 1976; HOUSTON AND HATFIELD, 1981). It would appear that this means a retention of the primitive state for this species.

The columbellid reproductive system combines very primitive features, like a gonopericardial-pallial communication, with advanced ones as it is the pouch for the resting penis. Based on this, MARCUS AND MARCUS (1962) divide the whole family into two groups: a) males with a seminal vesicle and no prostate, and females with an albumen gland and sperm storing organ; b) absence of seminal vesicle and presence of prostate in males combined with absence of albumen gland and sperm storing organ in females (sperm is kept in the pericardium).

None of the species studied presents either a bursa copulatrix or a prostate gland. This means that they wouldn't very well fit neither of the morphological divisions defined above. Interesting is also the fact that in spite of having an open male duct, *C. clavulus* has a higher compartmentalized reproductive system, whereas the other two species have a more generalized, with less distinct accessory structures, system. Whereas this means a more or less advanced condition it is difficult to say.

The greater similitude between *Bifurcium* and *Sincola* is especially interesting. These genera first appear in the early Miocene in fossil deposits of the Dominican Republic, Caribbean Sea. On the other hand, *Clavistrombina* is a recent genus of the eastern Pacific. Whereas these differences in times of origination could bear on the internal anatomy of the taxa is difficult to know. Many more studies of other species of these and other genera of the group are still needed in order to be able to make definite conclusions about the functional and ecological relationships of the reproductive systems and their evolution.

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